
Ixia acaulis, a New Acaulescent Species of Iridaceae: Ixioideae from the Knersvlakte, Namaqualand, South Africa

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ABSTRACT. The generic placement of a new species, *Ixia acaulis*, from limestone outcrops in the Knersvlakte, Vanrhynsdorp District, South Africa, is not immediately clear in part due to its reduced acaulescent habit. The bright yellow flowers have a subterranean ovary and are borne above ground level on a long perianth tube. An acaulescent habit is unusual in Iridaceae, although known in several genera of the two larger subfamilies, Iridoideae and Ixioideae. In an effort to correctly assign the plant to a genus, we have examined leaf anatomy and chromosome cytology as well as macromorphology and palynology. A basal rooting corm places the species firmly in Ixioideae, as does the perforate exine sculpturing. We conclude that it belongs in the southern African genus *Ixia*, although an acaulescent habit is otherwise unknown in this genus and other aspects of the plant do not exactly conform to this genus.

The uncertain generic position of a new species of Iridaceae subfamily Ixioideae from the Knersvlakte north of Vanrhynsdorp, Cape Province, South Africa, required detailed investigation of its morphology, leaf anatomy, cytology, and palynology. It is unusual in the subfamily in lacking an aerial stem. The flower has a subterranean ovary and is raised above the ground by means of a long perianth tube. Finely fibrous corm tunics seem to preclude any relationship with *Hesperantha*, *Romulea*, or *Syringodea*, in which acaulescence is the rule or at least not uncommon, but in which the corm tunics are more or less woody. However, a combination of reduced and specialized features makes it uncertain whether the species belongs in *Ixia*, *Tritonia*, *Sparaxis*, *Anomatheca*, or *Duthieastrum*, all of which have fibrous corm tunics, but only the last is normally acaulescent.

MORPHOLOGY

VEGETATIVE ORGANIZATION

The small plants (Fig. 1A, B) grow singly or in small clumps, each individual consisting of an elongate, more or less symmetrical, round-based corm with fibrous corm tunics (Fig. 1B) that accumulate in older plants to form a thick matted fibrous layer. The corms produce roots from the basal area but in no particular pattern. The 3–5 foliage leaves are basal and sheathed below the ground by 2 membranous, entirely sheathing cataphylls. The leaf blades are equitant and more or less linear. Under natural conditions the blades are more or less prostrate on the ground. Although the blades are unifacial, there is no morphological or anatomical differentiation between the leaf surfaces facing toward or away from the surface of the ground. Grown under greenhouse conditions with more water than normally available (as were the plants illustrated), the leaves tend to be inclined rather than prostrate. The stem is short, 1–2 cm long, but does not reach ground level at anthesis and bears one or occasionally two flowers. As the capsules ripen the peduncle elongates so that the seeds are released at ground level.

FLORAL STRUCTURE

The flowers are sessile (i.e., lack pedicels) and are subtended by a pair of opposed membranous bracts inserted at the base of the ovary (Fig. 1C, G), thus conforming to the pattern in all Ixioideae. In the three other subfamilies of Iridaceae the flowers are normally pedicellate, rarely sessile, and always subtended by a single bract (Goldblatt, 1990). Also typical of Ixioideae, the outer bract is larger than the inner in *Ixia acaulis*, although the two bracts are more or less equal in length (Fig. 1G). The inner bract is 2-veined and apically forked. The

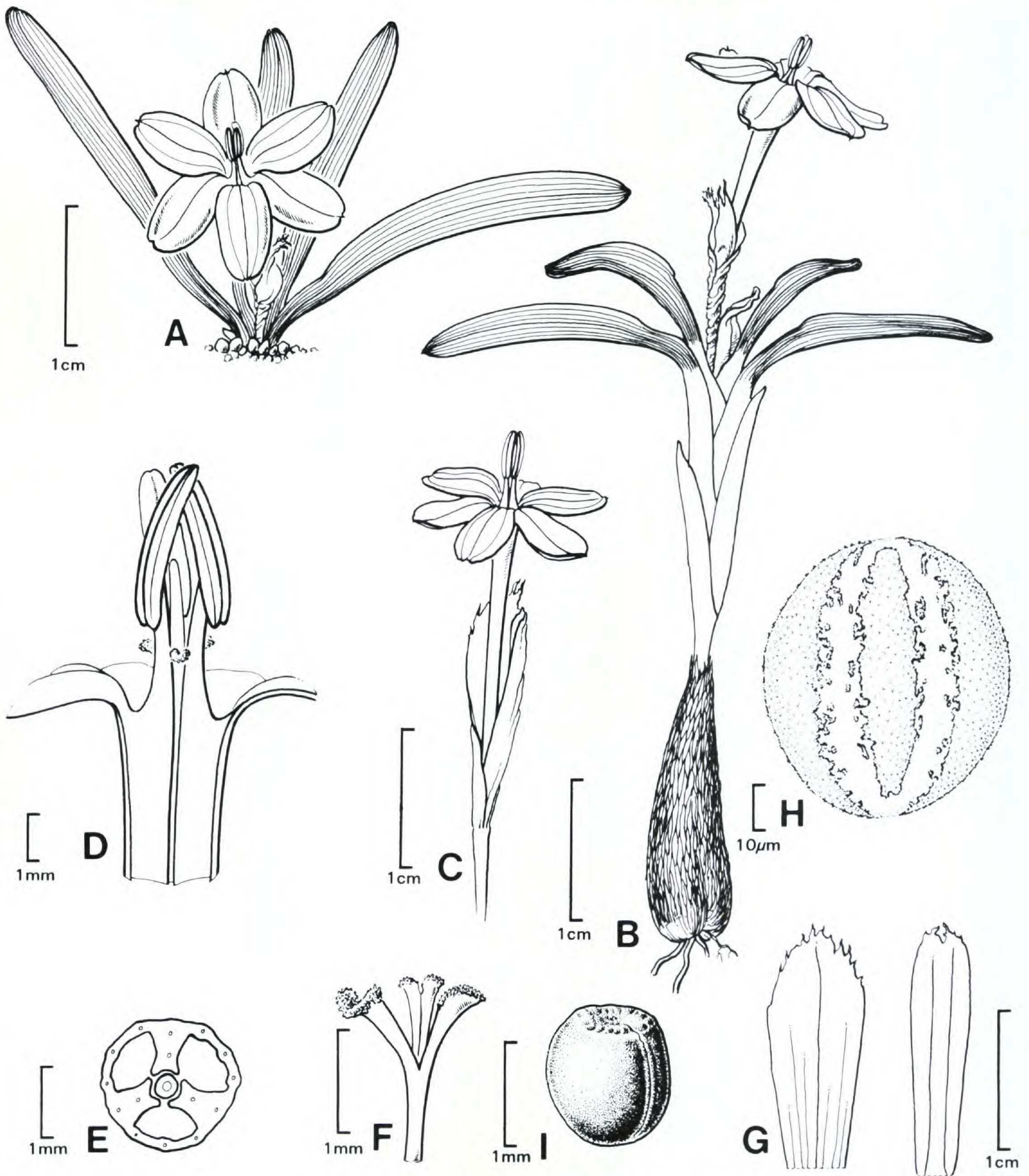


Figure 1. *Ixia acaulis* Goldblatt & J. Manning. —A. Habit. —B. Entire plant with corm. —C. Flower and paired bracts and apex of stem. —D. Longitudinal section of upper half of flower. —E. Transverse section of perianth tube at mid level showing filament flanges and central style. —F. Detail of style branches. —G. Detail of outer and inner bracts. —H. Polar view of pollen grain with operculum lying over the aperture. —I. Seed. (Drawn by J. C. Manning.)

ovary is subterranean and the flower is raised above the ground by a long perianth tube, 15–20 mm long, that reaches about 10 mm above ground. The flower is actinomorphic and the bright yellow tepals are subequal and spread at right angles to the tube (Fig. 1B, C). The short filaments are exerted ca. 1.5 mm from the perianth (Fig. 1D) and are de-

current, extending to the middle of the tube as flanges that reach almost to the center of the tube (Fig. 1D, E). The filiform style reaches to about the mouth of the tube where it divides into three short branches, ca. 1 mm long, and each branch is adaxially channeled above, but the margins are conduplicate below so that the lower two-thirds are tubular

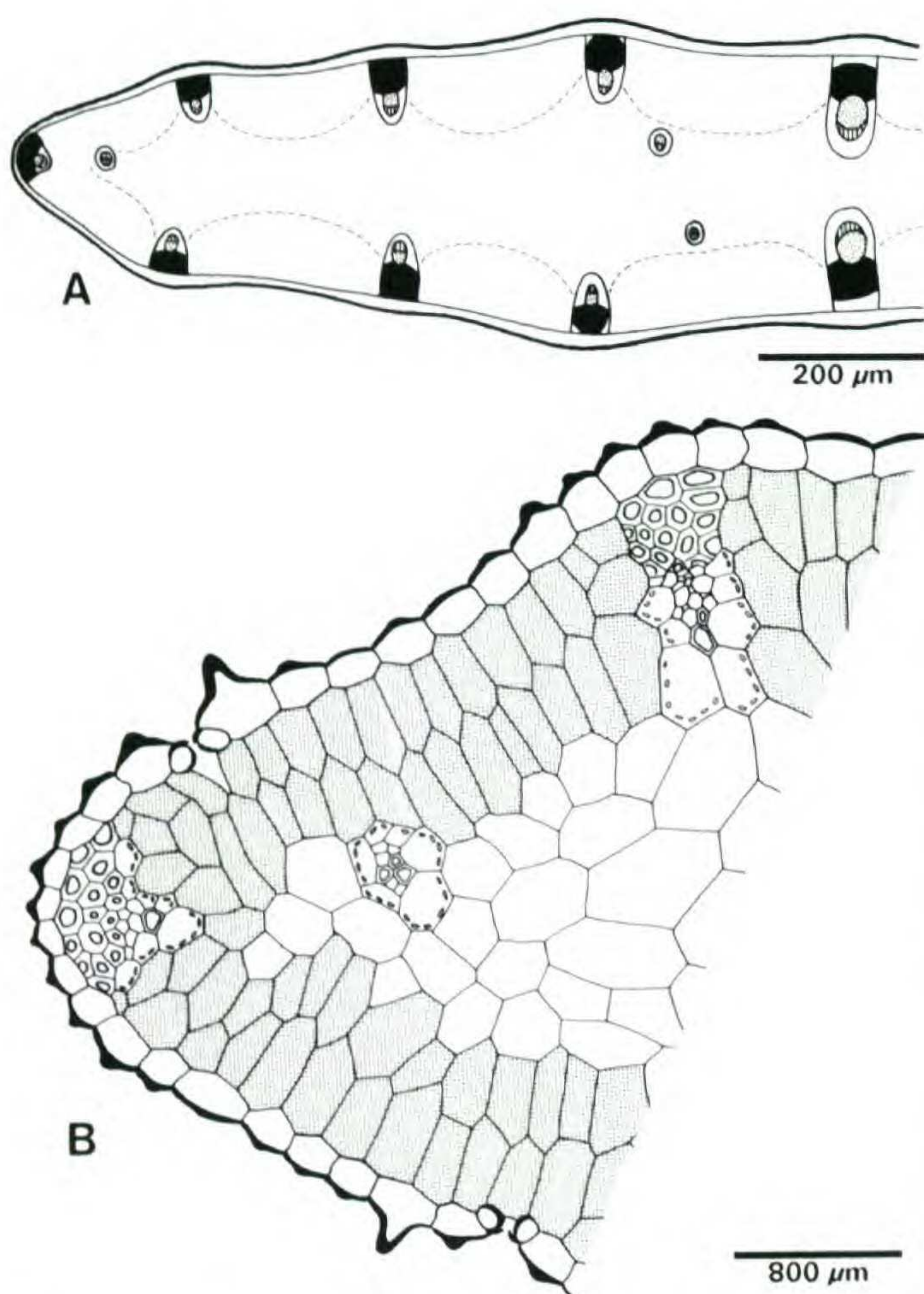


Figure 2. Transverse section of leaf of *Ixia acaulis*. — A. Tissue distribution in half leaf (pseudomidrib vein pair to margin). — B. Cell detail of marginal area (palisade mesophyll shaded). (Drawn by J. C. Manning.)

(Fig. 1F). The stigmatic tips of the style branches emerge between the adjacent filaments a short distance below the base of the anthers (Fig. 1D). The erect and more or less parallel anthers are linear-oblong, submedianly fixed, and longitudinally dehiscent (Fig. 1D).

FRUIT AND SEED

The fruit is a globose capsule with somewhat cartilaginous walls, corresponding to the presumed plesiomorphic state for Ixioideae. The seeds are globose, extremely hard, and lack primary or secondary sculpturing (Fig. 1I). The only notable feature is the white filiform vestige of the ovular vasculature lying over the raphe, thus outside the body of the mature seed. This seed type is derived in shape, absence of surface sculpturing, and in the peculiar excluded vascular trace (Manning & Goldblatt, in prep.). Similar hard rounded seeds without primary or secondary sculpturing characterize several genera of Ixioideae tribe Ixieae, among them *Sparaxis*, *Ixia*, *Dierama*, *Duthieastrum*, *Tritonia*, its close allies *Crocosmia*, *Chasmanthe*, and *Devia* (de Vos, 1974; Goldblatt & Manning, 1990; in prep.), as well as *Freesia* and most species of *Anomatheca*. The two

latter have a characteristically inflated raphe (Goldblatt & Manning, in prep.) and do not have the excluded vascular trace that occurs in the other genera listed above (seeds of *Duthieastrum* are unknown in this respect).

LEAF ANATOMY

In cross section (Fig. 2) the blades of the unifacial leaves are oblong and conform to the basic pattern for Iridaceae (Arber, 1921; Rudall & Goldblatt, 1989) in having vascular bundles in two opposed rows, with the phloem directed toward the epidermis and the xylem toward the interior of the leaf. The median pair of veins are slightly larger than the others and thus constitute a pseudomidrib, generally visible as such in surface view. The epidermal cells are slightly wider than high and papillate; the marginal epidermal cells are similar to those of the laminar surface except in their slightly smaller size (Fig. 2B). Stomata are sunken and the guard cells are small. Immediately below the marginal epidermis there is a small strand of sclerenchyma (= phloem cap) contiguous with the phloem of a small marginal vein. There is a well-developed palisade two cell layers thick and a sclerenchyma phloem cap on all primary and secondary bundles reaching the epidermis in all bundles except the median pair. The bundle sheaths are unthickened except at the phloem pole. Presence of submarginal sclerenchyma associated with a marginal vein is probably plesiomorphic for Ixioideae (Rudall & Goldblatt, 1989; Goldblatt, 1990), and a pseudomidrib is plesiomorphic for tribe Ixieae. The leaf anatomy thus corresponds with the basal condition for Ixieae (Rudall & Goldblatt, 1989), including *Ixia* and *Dierama* among genera possibly closely related to the new species.

A derived leaf margin anatomy in which the leaf margin cells are columnar and heavily thickened on the anticlinal walls and the margins lack subepidermal sclerenchyma characterizes *Tritonia* (excepting *T. marlothii* and *T. delpierrei*) (de Vos, 1980), *Sparaxis* (including *Synnotia*), *Anomatheca*, and a few more genera (Rudall & Goldblatt, 1989). *Duthieastrum* has leaves without either subepidermal marginal sclerenchyma or columnar marginal epidermal cells with thickened walls, but it does have a marginal vein (Goldblatt, unpublished).

POLLEN GRAINS

The pollen grains (Fig. 1H), examined in the fully expanded state in 1% aceto-orcein, are monosulcate and rounded, ca. $62 \times 54 \mu\text{m}$, thus slightly longer in the plane of the sulcus. The sulcus has a conspicuous, narrowly elliptic operculum lying across

the long axis and nearly as long as the sulcus and ca. 12 μm wide in the midline. The exine is perforate with the surface bearing scattered small spinulae. Both in the presence of an operculum and in the perforate and sparsely spinulate exine the species corresponds with the plesiomorphic state for Ixioideae (Goldblatt, 1990). In the presumed plesiomorphic condition for the subfamily, also the most common, the operculum is double-banded (Goldblatt et al., 1991). A derived single-banded operculum is so far known only in *Ixia*, some species of *Anomatheca* (Ixieae), and *Lapeirousia* and *Thereianthus* (Watsonieae) (Goldblatt et al., 1991; Goldblatt & Manning, in prep.). Apparently only in *Ixia* is the operculum consistently single-banded, although only a selection of species have so far been examined. The grains are some 30% larger than recorded in other species of *Ixia* (Goldblatt et al., 1991), possibly related to the long perianth tube and consequent need for larger reserves to permit growth through a longer style.

CHROMOSOME CYTOLOGY

Root tips (examined by M. Takei), harvested from sprouting corms and treated as described by Goldblatt et al. (1993), showed a diploid chromosome number of $2n = 20$ at mitotic metaphase. The chromosomes are relatively small, the longest four pairs 2.7–2.3 μm and the smaller pairs 1.8–1.2 μm long, and asymmetric in arm ratio. The second longest and one of the shorter pairs are nearly metacentric, and the rest are acrocentric to submetacentric. The karyotype is weakly bimodal with three longer pairs standing out from the remaining shorter chromosomes. Satellites were not seen clearly but appear to be small and located on one of the longer chromosome pairs. Other Ixioideae with a base number of $x = 10$ (Goldblatt, 1971; de Vos, 1974) include *Ixia*, *Dierama*, *Sparaxis* (including *Synnotia*), and *Duthieastrum* (all Ixieae) and *Thereianthus*, *Micranthus*, and section *Fastigiata* of *Lapeirousia* (Watsonieae) and *Pillansia*, only genus of Pillansieae. The ancestral base number for Ixioideae may be $x = 10$. In general size the chromosomes of *Ixia* correspond most closely with those of the new species. Chromosomes of *Sparaxis* are some 20% smaller (total chromosome length) (Goldblatt & Takei, in prep.) and exhibit no bimodality.

DISCUSSION

GENERIC POSITION

A basally rooting corm, long-lasting flowers with a well-developed perianth tube, paired bracts in-

serted below a sessile ovary, operculate pollen grains, and perforate exine, synapomorphies for Ixioideae (Goldblatt, 1991; Goldblatt et al., 1991), are all present in *Ixia acaulis* and confirm its subfamilial position. Within Ixioideae it corresponds with Ixieae and Watsonieae in having leaves with a pseudomidrib. Association with Watsonieae may be excluded because members of this tribe have corms that develop entirely from an axillary bud (the new corm lies lateral to the flowering stem), and they also have deeply divided style branches, the former possibly apomorphic and the latter almost certainly so (Goldblatt, 1990, 1991). There is little doubt that the new species belongs in Ixieae. Among the 20 genera of the tribe, the new species has similarities with several genera, especially *Tritonia*, *Duthieastrum*, *Anomatheca*, and *Ixia*, although the acaulescent condition and subterranean ovary are atypical of all but the monotypic *Duthieastrum*. Only one species of *Tritonia*, *T. florentiae* (E. Phillips) Goldblatt, lacks an aerial stem, but no acaulescent species of *Ixia* or *Anomatheca* are known. Acaulescence has apparently evolved repeatedly in Iridaceae and frequently in Ixioideae, in which at least some species of *Lapeirousia* and *Hesperantha*, most species of *Romulea*, and all of *Syringodea* and *Crocus* (as well as *Duthieastrum*) lack an aerial stem at anthesis. Acaulescence, especially common in African Ixioideae among species of arid and semiarid areas, is obviously of direct adaptive significance, and alone is probably of little or no value in considering the relationships of species of Ixieae.

More important in determining relationships among Ixioideae are the nature of the style branches (either simple or deeply divided), leaf margin anatomy, bract texture (green and herbaceous or membranous and transparent or scarious), seed morphology, and possibly pollen grain morphology. The most likely generic position for this new species seems to us to be *Ixia*, with which it corresponds mainly in plesiomorphic features (unspecialized leaf anatomy, chromosome number, simple style branches); it also shares a notable synapomorphy with *Ixia*, pollen grains with a single-banded operculum. The membranous and transparent bracts may also be apomorphic for *Ixia*.

In some species of *Ixia* alone of the genera of Ixioideae, the style divides at the mouth of the perianth tube and has short branches (in *Hesperantha* the style consistently divides at or below the mouth of the tube but the branches are long and trailing). The new species does not accord with *Anomatheca*, *Tritonia*, *Duthieastrum*, or *Sparaxis* in leaf margin anatomy or pollen grain structure. These four genera have columnar marginal epidermal cells

and, except for *Duthieastrum*, lack submarginal sclerenchyma whereas their pollen grains have double-banded opercula. Additionally, the style branches of *Anomatheca* are always deeply divided, and the seeds of this genus do not have an excluded vascular trace. Basic chromosome number in *Sparaxis* is also $x = 10$, but both *Tritonia* and *Anomatheca* have $x = 11$, excepting one derived species of *Tritonia*, *T. florentiae*, which has the secondary base of $x = 10$ (Goldblatt & Takei, in prep.).

RELATIONSHIPS WITHIN IXIA

Ixia subg. *Dichone* is derived in the genus in its peculiar, stout, and so-called subdidymous anthers (Lewis, 1962), which appear to lack a connective and are additionally normally (possibly always) basally porate. The six species of the subgenus also always have pink flowers and, according to Lewis (1962), involute style branches. Thus, *I. acaulis* falls within the remaining subgenus *Ixia*, where it accords best with section *Hyalis* and *Morphixia*. It may be most closely related to *I. paucifolia* of the latter (de Vos, pers. comm.), which also has a long perianth tube, and included, decurrent filaments. In one aspect, however, *I. acaulis* seems to differ from *Ixia*: it has subcentrally fixed anthers, whereas near basifixed anthers are characteristic of the genus, according to de Vos (pers. comm.).

SYSTEMATICS

Ixia acaulis Goldblatt & J. Manning, sp. nov.

TYPE: South Africa. Cape: 31.18 (Vanrhynsdorp) Knersvlakte, farm Rooiberg, low limestone ridges (BC), 19 May 1992, *Snijman & Manning 1249* (holotype, NBG; isotypes, MO, PRE). Figure 1.

Plantae 2–3 cm altae, interdum caespitosae, cormo elongato, tunicis fibrosis, foliis productis 3–5, laminis lineato-lanceolatis 2–4 mm latis, floribus solitaris actinomorphae flavis, tubo perianthii 15–20 mm longo, tepalis aequalibus ovato-oblongis 6–7 × 3 mm, filamentis erectis ca. 1.5 mm longis, antheris lineari-oblongis erectis contiguis ca. 2 mm longis, stylo diviso prope apicem tubi, ramis styli ca. 1 mm longis.

Plants acaulescent, often growing in small clumps, leaves and flowers reaching 2–3 cm above the ground. *Corm* elongate, ca. 3–4 mm wide near the base, tapering above, ca. 15 mm long, the tunics moderately to finely fibrous and with age accumulating as a dense covering. *Foliage leaves* 3–5, all basal, sheathed below by 1–2 transparent cataphylls, these just reaching ground level; leaf blades linear to narrowly lanceolate, ca. 1.5–2 mm wide, often prostrate, or inclined toward the ground, ± obtusely

acuminate. *Stem* subterranean, 9–18 mm long, usually unbranched or with one branch. *Inflorescence* a solitary flower (or the flowers solitary on each branch); *bracts* membranous, the outer larger, ca. 10 mm long, somewhat fringed along the upper margin, inner bract about as long but narrower, 2-veined and lightly forked apically, reaching to 5 mm above the ground. *Flowers* actinomorphic, bright yellow, whitish in the tube; *perianth tube* 15–20 mm long, arising below ground level and extending to 10 mm above the ground, cylindrical, widening gradually above; *tepals* subequal, oblong-ovate, obtuse to emarginate, 6–7 × 3 mm, spreading at right angles to the tube. *Stamens* erect, the filaments arising at the top of the tube, ca. 1.5 mm long, decurrent and forming prominent ridges reaching downward to the middle of the tube, the ridges extending inward to the style but not joined to it; *anthers* linear-oblong, longitudinally dehiscent, subcentrally fixed, erect and ± contiguous, ca. 2 mm long. *Ovary* oblong, ca. 2.5 mm long; *style* filiform, dividing at or just beyond the mouth of the tube, the branches short, ca. 1 mm long, the apices emerging between the filaments, terminally stigmatic, adaxially channeled in the upper part but the margins conduplicate below and the branches thus tubular in the lower half. *Capsules* globose, 5–6.5 mm long, borne at ground level. *Seeds* few per locule (usually 3–4), globose, smooth, dark red-brown, ca. 1.5 mm diam., the vascular trace excluded and often persisting as a white strand along the raphe. *Chromosome number* $2n = 20$.

DISTRIBUTION AND HABITAT

Ixia acaulis appears to be restricted to limestone ridges, clearly a specialized habitat, in the arid Knersvlakte of southern Namaqualand. This area of low rainfall, less than 100 mm p.a., normally falling in the winter months, is known for its diversity of habitats and extreme local endemism, particularly among Aizoaceae–Mesembryanthemoideae. Iridaceae are not well represented here, but other Knersvlakte endemics in the family include *Homeria maximiliani* Schlechter, *Moraea deserticola* Goldblatt (both Iridoideae), and *Lapeirousia angustifolia* Schlechter (if this is regarded as distinct from the related *L. pyramidalis* (Lamarck) Goldblatt). Among these Iridaceae, *I. acaulis* is unusual in flowering at the beginning of the wet season in May (and possibly June) rather than in the early spring in July and August. This unusual flowering time as well as the specialized habitat together account for its late discovery in an area that has been explored botanically since the late 19th century. So far, *I.*

acaulis is known from two limestone ridges on the farm Rooiberg just to the north of the Saldanha-Sishen rail line. It grows in rock cracks or wedged between boulders in a virtually lithophytic situation. The few other limestone outcrops in the Knersvlakte, an area of predominantly fine clay soils often covered by a dense superficial layer of quartz pebbles, remain to be examined for the presence of the species.

Paratypes. SOUTH AFRICA. **Cape Province:** 3118 (Vanrhynsdorp) Knersvlakte, Farm Rooiberg, low limestone ridges (BC), Perry, 1991 (NBG), 27 Aug. 1991 (fr), Goldblatt & Manning 9132 (MO, NBG, PRE).

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